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BIRD COMMUNITIES AFTER BLOWDOWN IN A LATE-SUCCESSIONAL GREAT LAKES SPRUCE-FIR FOREST

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ABSTRACT.—In 2001 and 2002, we inventoried the bird communities and vegetation of two 6.25-ha plots in a late-successional spruce-fir (*Picea mariana–Abies balsamea*) forest of northern Minnesota that was severely disturbed by a 1999 windstorm. We compared these results with those from two nearby plots that were largely unaffected by the storm. Using vegetation data collected from one of the two plots in each location before the disturbance in 1996 and 1998, we examined similarities between plots before and after the storm. The most significant effect of the storm on vegetation was a ≥80% decrease in tree cover and a >100% increase in shrub-layer structure because of trees that were tipped over or snapped off. Of 30 territorial bird species, 9 held territories exclusively in the blowdown, while 2 held territories exclusively in the control. By foraging guild, 10 of 11 (91%) species of ground-brush foragers had more territory cover in the blowdown, while 7 of 13 (54%) species of tree-foliage searchers had more territory cover in the control. Black-and-white Warbler (*Mniotilta varia*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Mourning Warbler (*Oporornis philadelphia*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), and Red-eyed Vireo (*Vireo olivaceus*) had significantly ($P < 0.05$) more territory cover in the blowdown, whereas Blackburnian Warbler (*Dendroica fusca*), Golden-crowned Kinglet (*Regulus satrapa*), and Yellow-rumped Warbler (*Dendroica coronata*) had more territory cover in the control. Canonical correspondence analysis revealed that differences in avian territory cover were primarily attributable to changes in vegetation structure, in particular the increase of structural debris on the ground and the reduction in tree canopy, occurring because of the wind. *Received 25 October 2004, accepted 30 August 2005.*

Forest composition and structure in the Upper Great Lakes region is greatly influenced by disturbances, primarily fire, insect outbreaks, logging, and wind (Van Wagner and Methven 1978, Bonan and Shugart 1989, Bergeron 1991, Drapeau et al. 2000). Although the most prevalent natural disturbances in this region are fire and insects, large-scale wind events that significantly reduce the canopy are believed to occur with average return intervals of 1,000 years or more (Frelich and Reich 1996, Larson and Waldron 2000, Frelich 2002). A number of studies have examined the effects of disturbances such as fire and logging on avian communities in the Upper Great Lakes region (Apfelbaum and Haney 1986, Schulte and Niemi 1998, Drapeau et al. 2000); however, despite its known impact on vegetation structure and composition (Frelich and Reich 1996), few researchers have examined the effects of wind (Smith and Dallman 1996, Dyer and Baird-Philip 1997).

On 4 July 1999, a microburst—known as a derecho, and characterized by straight-line winds in excess of 145 km/hr—disturbed approximately 200,000 ha in northeastern Minnesota (USDA Forest Service 2002). We documented the effects of severe wind disturbance by comparing post-disturbance vegetation and bird communities on two blowdown plots with two nearby control plots that had the same disturbance history and vegetation structure before the storm. Because bird species composition is closely related to habitat structure (Karr and Roth 1971, Willson 1974, Niemi and Hanowski 1984, Pearman 2002), and because the wind reduced tree cover by more than 80%, with a corresponding increase in shrub-layer structure and coarse woody debris from tipped trees and snapped tree-tops, we expected a community shift from one dominated by tree-foliage searchers to one dominated by ground-brush foragers. We expected responses similar to those following fire (Apfelbaum and Haney 1981, Morissette et al. 2002) and, in some cases, timber harvesting (Hobson and Schieck 1999, Lohr et al. 2002).

METHODS

We conducted our study in a 200-year-old black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) forest that originated from

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an 1801 stand-replacing wildfire (M. L. Heinselman pers. comm.) in northeastern Minnesota's Superior National Forest (Fig. 1). Two blowdown study plots were located on Seagull Lake (48° 07′ N, 90° 54′ W) and two control plots, minimally affected by the 4 July 1999 storm, were located near Red Rock Bay (Saganaga Lake), approximately 10 km to the northwest of Seagull Lake. Each 250 × 250-m (6.25 ha) study plot, surrounded by a 25-m buffer zone to reduce the effects of edge, was subdivided with flagging into a grid of 50 × 50-m cells. Using previously collected data from one of the blowdown plots (1996) and one of the control plots (1998), we employed a BACI design (Before, After, Control, Impact; Stewart-Oaten et al. 1986, Irons et al. 2000, Stewart-Oaten and Bence 2001) to better illustrate similarities between plots before the disturbance, and changes occurring because of the windstorm. We did not use a BACI design to analyze our bird data, however, because the annual variation in bird populations is unpredictable (Blake et al. 1994, Collins 2001) and our pre-disturbance avian surveys were conducted in different years.

Post-blowdown vegetation surveys were conducted in 2001 and again in 2002 along 50-m transects running through the center of 10 randomly selected grid cells in each of the four study plots (n = 4 plots/year × 10 cells/plot × 2 years = 80). Using the same methodology, we surveyed vegetation in one of the pre-blowdown plots in 1996 and one of the control plots in 1998 (n = 2 plots × 10 cells/plot = 20). Tree and shrub cover for each species were estimated using the line intercept method (Canfield 1941). Trees were defined as stems standing <45 degrees from vertical with a diameter at breast height (dbh) ≥5 cm. Shrubs were identified as all stems >1 m tall and <5 cm dbh or as live trees standing >45 degrees from vertical. Dead trees were considered coarse litter if standing >45 degrees from vertical and snags if standing <45 degrees. After the storm, diameters of all stems >5 cm that crossed the 50-m intercept line were recorded and used to estimate the volume of coarse woody debris per unit area.

We estimated tree and shrub density by recording the number and diameter (rounded to the nearest 5 cm) of live and dead trees rooted within 1 m of either side of the transect and the number of live and dead shrub stems within 1 m of the right side of the transect. We used five 1-m^2 circular plots centered at 5, 15, 25, 35, and 45 m along the transect line to estimate percent cover of herbs (height <1 m), exposed mineral (e.g., rock, bare soil), bryophytes, coarse litter (diameter >5 cm), and fine litter (diameter <5 cm).

We conducted bird surveys on each of the four plots once per morning for each of 5 days during May–mid-June 2001 and 2002. Surveys were performed using a modification of Kendeigh's flush-plot techniques (Kendeigh 1944, Apfelbaum and Haney 1986). Each survey was conducted by one or two experienced birders who plotted on data sheets all birds seen or heard from grid-cell vertices. Surveys, which were restricted to days without significant wind or rain, averaged about 6 person-hr, each designed to plot every territorial male using the area.

After the completion of all five daily surveys, bird locations for each plot were compiled onto summary sheets. Territories were delineated from clusters of survey registrations and other evidence of established territories, such as active nests, or adults carrying food or fecal sacs. We considered likely transients, or individuals with territories too large to determine with our method, as visitors (V) unless they were recorded in the same location on at least 3 of the 5 survey days.

Data analyses.—To address issues of spatial dependence within the vegetation dataset, we first eliminated repeatedly sampled grid cells while balancing sample sizes between years and plots. Of the 100 grid cells for which we had vegetation data, we retained 62 cells (10 pre-blowdown [1996], 10 pre-blowdown control [1998], 12 post-blowdown [2001], 11 post-blowdown control [2001], 9 post-blowdown [2002], 10 post-blowdown control [2002]) for further analysis. Next, we examined the resulting vegetation data for normality (Q-Q plot and Shapiro-Wilk tests) and homogeneity of variance (Levene's test) and transformed data according to Box-Cox plots (Box and Cox 1964) as necessary. Finally, we used a two-way analysis of variance (ANOVA) for each habitat variable (n = 19) to examine differences based both on plot type (blowdown or control) and time (1996 or 1998, 2001, 2002). If the ANOVA yielded a

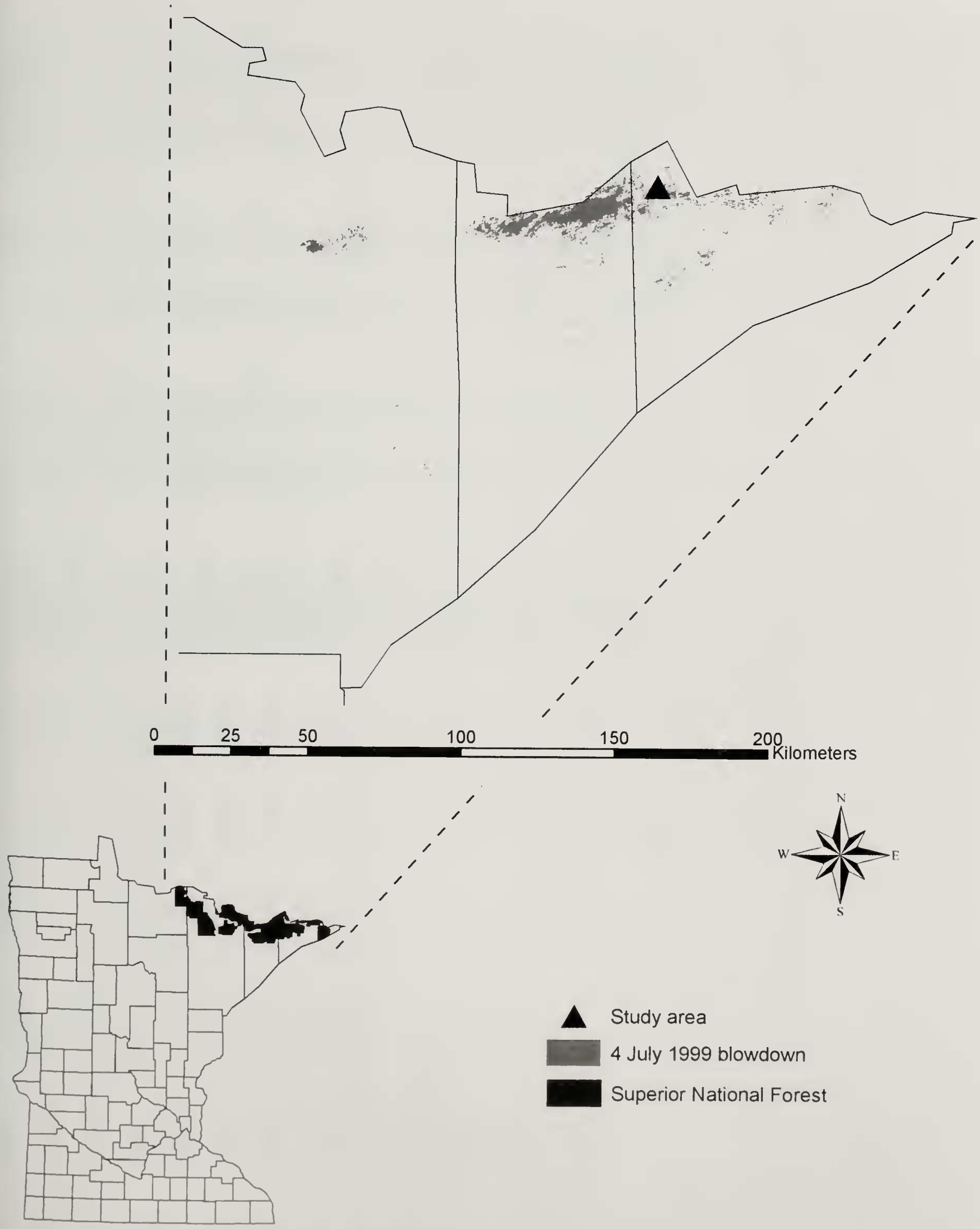

FIG. 1. Location of the study area and the blowdown area in northeastern Minnesota's Superior National Forest. The blowdown occurred 4 July 1999, a result of a >145 km/hr microburst.

TABLE 1. Mean vegetation characteristics (±SE) and outcomes of two-way ANOVA on 62 (31 control, 31 blowdown) 50-m transects before (1996 or 1998)[a] and after (2001, 2002) a catastrophic blowdown in a black spruce–balsam fir forest in the Superior National Forest, Minnesota. When ANOVA (site × time) yielded a significant interaction ($P < 0.05$), simple main effects analyses were conducted, followed by pairwise comparisons to examine differences between the blowdown and control plots. Asterisks indicate a significant difference (Bonferroni: $\alpha = 0.025$) between plot types in the given year (column), while different capital letters indicate significant differences (Bonferroni: $\alpha = 0.008$) between years in the given plot type (row). There were no significant differences between years for control plots. CBRYO = % bryophyte cover; CCOLIT = % coarse litter cover; CFILIT = % fine litter cover; CHERB = % herb cover; CMINRL = % mineral cover; CSHRB = % shrub cover; CSHRBD = % deciduous shrub cover; CSHRBE = % evergreen shrub cover; CTREE = % tree cover; CTREED = % deciduous tree cover; CTREEE = % evergreen tree cover; CVR = % shrub or tree cover; DEBRIS = coarse woody debris (m^3); DEDDIA = dead tree diameter (cm); DEDSHR = dead shrub stems; DEDTRE = dead trees; LIVDIA = live tree diameter (cm); LIVSHR = live shrub stems; LIVTRE = live trees.

Vegetation variable	ANOVA						Plot type	Mean		
	Site		Time		Site × Time			Pre-blowdown 199x[a]	Post-blowdown 2001	Post-blowdown 2002
	F	*P*	*F*	*P*	*F*	*P*				
CBRYO[b,d]	1.30	0.26	0.20	0.82	2.38	0.10	Control	39.3 ± 5.83	52.6 ± 6.91	34.6 ± 7.62
							Blowdown	38.6 ± 5.65	29.7 ± 6.44	39.1 ± 8.60
CCOLIT[b,d]	1.34	0.25	0.40	0.67	1.43	0.25	Control	12.0 ± 2.22	14.0 ± 3.12	14.3 ± 2.70
							Blowdown	19.8 ± 3.10	16.0 ± 2.90	12.4 ± 1.94
CFILIT[d]	0.89	0.35	5.48	0.007	0.77	0.47	Control	32.7 ± 2.96	57.4 ± 8.47	60.2 ± 7.00
							Blowdown	47.0 ± 6.20	60.9 ± 7.64	57.8 ± 4.14
CHERB[d]	0.52	0.47	0.67	0.52	1.43	0.25	Control	38.1 ± 5.34	28.9 ± 4.75	26.9 ± 3.79
							Blowdown	27.7 ± 2.91	27.9 ± 3.43	31.0 ± 4.97
CMINRL[c,d]	0.01	0.93	6.16	0.004	0.94	0.40	Control	3.0 ± 1.55	1.7 ± 0.71	6.0 ± 2.58
							Blowdown	0.62 ± 0.30	2.3 ± 0.84	8.2 ± 2.89
CSHRB[d]	7.74	0.007	4.17	0.021	3.29	0.045	Control	44.1 ± 5.06*	45.3 ± 3.96	42.8 ± 5.78
							Blowdown	22.6 ± 2.04*A	46.5 ± 5.15B	32.2 ± 3.45AB
CSHRBD[d]	3.14	0.082	6.75	0.002	0.26	0.77	Control	6.8 ± 2.12	18.3 ± 3.52	17.3 ± 6.13
							Blowdown	11.1 ± 1.86	27.0 ± 4.03	21.2 ± 3.40
CSHRBE[d]	36.71	<0.001	2.58	0.085	1.78	0.18	Control	34.1 ± 3.80	33.8 ± 4.09	31.2 ± 3.67
							Blowdown	12.4 ± 2.10	23.9 ± 3.60	12.1 ± 1.76
CTREE[b,d]	11.37	0.001	11.71	<0.001	9.95	<0.001	Control	40.1 ± 4.38*	42.9 ± 5.47*	37.6 ± 6.08*
							Blowdown	51.6 ± 3.75*A	23.4 ± 5.07*B	7.6 ± 3.23*B
CTREED[c,d]	0.23	0.63	6.78	0.002	1.42	0.25	Control	19.0 ± 4.96	16.4 ± 5.90	10.3 ± 2.22
							Blowdown	24.2 ± 3.45	14.0 ± 3.94	2.9 ± 2.74
CTREEE[b,d]	16.32	<0.001	5.38	0.007	9.23	<0.001	Control	26.0 ± 2.26	32.0 ± 4.30*	29.1 ± 7.03*
							Blowdown	33.1 ± 4.48A	10.5 ± 2.47*B	5.0 ± 1.43*B
CVR[d]	13.71	<0.001	4.49	0.016	3.39	0.041	Control	67.7 ± 4.69	67.9 ± 4.87	66.1 ± 5.44*
							Blowdown	62.8 ± 3.30A	58.6 ± 4.69A	37.6 ± 4.71*B
DEBRIS[b,f]	14.94	<0.001	1.73	0.20	1.36	0.25	Control	no data	57.3 ± 12.35	33.6 ± 8.78
							Blowdown	no data	93.3 ± 15.43	89.4 ± 14.05
DEDDIA[d]	8.68	0.005	0.79	0.46	0.02	0.98	Control	10.8 ± 1.86	13.5 ± 1.82	14.7 ± 3.23
							Blowdown	17.9 ± 2.22	20.0 ± 2.70	20.7 ± 3.68
DEDSHR[c,d]	3.79	0.057	3.99	0.024	1.30	0.28	Control	6.1 ± 1.29	3.1 ± 0.81	2.0 ± 0.60
							Blowdown	3.4 ± 1.22	1.3 ± 0.45	2.2 ± 0.89

TABLE 1. Continued.

Vegetation variable	ANOVA							Mean		
	Site		Time		Site × Time					
	F	*P*	*F*	*P*	*F*	*P*	Plot type	Pre-blowdown 199x^a	Post-blowdown 2001	Post-blowdown 2002
DEDTRE^{b,d}	1.42	0.24	2.42	0.098	2.15	0.13	Control	4.3 ± 1.01	3.6 ± 1.17	1.3 ± 0.42
							Blowdown	2.2 ± 0.47	2.0 ± 0.37	2.1 ± 0.59
LIVDIA^c	0.91	0.34	7.81	0.001	8.90	<0.001	Control	11.4 ± 0.90*	11.6 ± 1.15*	11.7 ± 0.75*
							Blowdown	15.6 ± 1.49*A	8.8 ± 0.67*B	7.9 ± 0.86*B
LIVSHR^d	0.14	0.71	4.77	0.012	1.50	0.23	Control	44.5 ± 8.16	53.0 ± 8.54	56.6 ± 10.9
							Blowdown	24.1 ± 3.67	55.3 ± 10.31	66.6 ± 9.25
LIVTRE^{c,d}	8.26	0.006	3.64	0.033	1.34	0.27	Control	12.0 ± 2.09	10.8 ± 1.76	12.1 ± 3.30
							Blowdown	10.9 ± 1.82	5.8 ± 1.17	3.3 ± 0.50

[a] Data were collected in 1996 on the (pre-) blowdown plot, and in 1998 on the control plot.
[b] Data were transformed using square root.
[c] Data were transformed using natural log.
[d] Site df = 1,56; time df = 2,56; site × time df = 2,56.
[e] Site df = 1,55; time df = 2,55; site × time df = 2,55.
[f] Site df = 1,38; time df = 1,38; site × time df = 1,38.

significant interaction, indicating that the blowdown and control plots were changing differently with time, we conducted main effects analyses to examine both differences between plot type in a given year and differences between years within each plot type. To control for Type I error across the two simple main effects, we used a Bonferroni correction procedure (Winer et al. 1991) and set alpha for each simple main effect at 0.025. If the simple main effect (time) was significant, follow-up pairwise comparisons between 1996, 1998, 2001, and 2002 were performed using a Bonferroni-adjusted alpha set at 0.008 (0.025/3) to identify time periods of significant change.

Because we wanted to correlate bird presence with habitat characteristics, we analyzed our bird data at the same scale as the vegetation data (50 × 50-m grid cell), rather than at the 250 × 250-m plot level. This was accomplished by selecting 42 grid cells equally distributed by both year (2001, 2002) and plot between the blowdown and control plots. To mitigate issues of spatial dependence, we required all of the selected cells within the same year to be a minimum of 50 m apart, and we did not select the same cell in successive years. So that we could later perform a joint analysis using both bird and vegetation data, we further required that selected grid cells were those for which we had also collected vegetation data in the same year. After cell selection, we recorded by species (based upon our territory maps) the percentage of each selected cell covered by a territory. For summary purposes, species were assigned to foraging guilds (e.g., tree-foliage searcher, timber gleaner) according to those described by Bock and Lynch (1970). Next, we tested these data for homogeneity of variance (Levene's test) and used a one-way ANOVA to test for the effect of disturbance. Although somewhat unconventional, distinguishing bird use by measuring the percentage of each cell covered by a territory allowed us to detect differences between plots on a finer scale—an attribute we felt was required, given the patchiness of the landscape following the blowdown. We are aware that changes in both avian density (Huxley 1934, Wiens et al. 1985) and habitat (Gill and Wolf 1975, Smith and Shugart 1987) may affect territory size, but upon finding little difference in average territory size between plot types (blowdown or control), we concluded that significant differences in territory cover per cell would likely be the result of more territories rather than territories of a larger size.

In examining the relationship between habitat structure and bird species composition, we used only the 42 grid cells (21 blowdown, 21 control) from 2001 and 2002 for which we had both vegetation and bird data. First, we used a Pearson correlation matrix along with principal components analysis (PCA) to minimize redundancy within the dataset, following the recommendations of ter Braak (1986, 1994) for subsequent canonical correspondence analysis (CCA). If ≥2 variables were strongly correlated ($r > 0.60$) within the correlation matrix, we kept only the habitat variable most strongly correlated with the first principal component (i.e., the variable explaining a greater amount of the variation within the data). Next, using the remaining variables (10 of 19), we performed PCA again to reduce the complexity of the dataset and summarize the habitat variables within the blowdown and control areas. Finally, we conducted CCA, performed by the PC-ORD statistical package (McCune and Mefford 1999), on the 10 selected habitat variables and 15 common bird species (those with territory cover in at least 10% of the 42 grid cells) to investigate more closely the relationship between habitat characteristics and the distribution of bird species. To determine the significance level of this relationship (ter Braak 1987), the CCA included a Monte Carlo test on the first two canonical functions, conducted with 1,000 permutations and using time of day as the source for randomization. Means are presented ± SE.

RESULTS

Twenty-six percent (5 of 19) of the habitat variables examined in the blowdown were significantly different after the storm in 2001 or 2002 when compared with pre-storm estimates collected in 1996 (Table 1). In contrast, there were no significant differences in habitat variables between years (1998, 2001, 2002) in the control. Percent tree cover (CTREE), which was somewhat higher in the to-be disturbed area before the storm (control: 40.1 ± 4.38, blowdown: 51.6 ± 3.75), was significantly greater in the control after the windstorm in both 2001 (control: 42.9 ± 5.47, blowdown: 23.4 ± 5.07) and 2002 (control: 37.6 ± 6.08, blowdown: 7.6 ± 3.23). A similar trend was observed in diameter of live trees (LIVDIA) in the blowdown area: mean diameter decreased by 2002 (7.9 ± 0.86) to only half that observed before the storm (15.6 ± 1.49). Whereas it was not significantly different before the storm, evergreen tree cover (CTREE) and shrub or tree cover (CVR) were also significantly greater in the control than in the blowdown after the disturbance. On the other hand, percent shrub cover (CSHRB) was significantly greater in the control before the blowdown (control: 44.1 ± 5.06, blowdown: 22.6 ± 2.04), but was not significantly different afterwards in either 2001 (control: 45.3 ± 3.96, blowdown: 46.5 ± 5.15) or 2002 (control: 42.8 ± 5.78, blowdown: 32.2 ± 3.45) due to tipped trees and broken-topped trees that were still alive in both years. The volume of coarse woody debris (DEBRIS)—the only variable that was not measured before the storm—was greater ($P < 0.001$) in the blowdown during both 2001 (control: 57.3 ± 12.35, blowdown: 93.3 ± 15.43) and 2002 (control: 33.6 ± 8.78, blowdown: 89.4 ± 14.05).

Of the 30 bird species with identified territories in either the blowdown or control, 18 had territories in both plot types. Two species had territories only in the control while nine species had territories exclusively in the blowdown. Seven territorial and visitor species recorded in the blowdown were not recorded in the control, whereas all species recorded in the control had territories or were recorded as visitors in the blowdown.

Species for which we detected a greater percentage of territory cover per grid cell in the blowdown included Black-and-white Warbler (scientific names listed in Table 2; control: 2.1 ± 1.49, blowdown: 13.3 ± 4.49, $F_{1,40} = 5.60$, $P = 0.023$), Chestnut-sided Warbler (control: 0, blowdown: 12.1 ± 4.35, $F_{1,40} = 7.81$, $P = 0.008$), and Mourning Warbler (control: 0, blowdown: 16.2 ± 5.72, $F_{1,40} = 8.01$, $P = 0.007$; Table 2). Species with a greater percentage of territory cover per cell in the control included Blackburnian Warbler (control: 20.5 ± 6.57, blowdown: 3.3 ± 1.90,

TABLE 2. Mean 2001 and 2002 percent bird territory cover per cell (±SE), bird frequency (number of cells with territory cover), and outcomes of one-way ANOVA between 21 blowdown and 21 control cells following a catastrophic 1999 blowdown in a black spruce–balsam fir forest in the Superior National Forest, Minnesota. Results are presented by foraging guild. Birds detected, but not considered territorial, were recorded as visitors (V).

Guild/Species	Mnemonic	Control[a]	Blowdown	Frequency	$F_{1,40}$	P
Flycatchers						
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	YBFC	4.5 ± 2.95	18.8 ± 5.84	12	4.76	0.035
Alder Flycatcher (*Empidonax alnorum*)	ALFC	—	6.2 ± 4.17	4	2.21	0.15
Least Flycatcher (*Empidonax minimus*)	LEFC	1.0 ± 0.95	6.4 ± 4.70	3	1.31	0.26
Ground-brush foragers						
Winter Wren (*Troglodytes troglodytes*)	WIWR	4.6 ± 2.05	13.1 ± 5.36	14	2.18	0.15
Swainson's Thrush (*Catharus ustulatus*)	SWTH	19.0 ± 6.25	12.4 ± 4.35	17	0.75	0.39
Hermit Thrush (*Catharus guttatus*)	HETH	1.0 ± 0.95	3.8 ± 3.34	3	0.68	0.42
Nashville Warbler (*Vermivora ruficapilla*)	NAWA	30.7 ± 7.68	17.6 ± 6.62	19	1.67	0.20
Chestnut-sided Warbler (*Dendroica pensylvanica*)	CSWA	—	12.1 ± 4.35	8	7.81	0.008
Ovenbird (*Seiurus aurocapilla*)	OVBI	—	1.9 ± 1.36	2	1.97	0.17
Northern Waterthrush (*Seiurus noveboracensis*)	NOWT	—	1.4 ± 1.43	1	1.00	0.32
Mourning Warbler (*Oporornis philadelphia*)	MOWA	V	16.2 ± 5.72	9	8.01	0.007
Chipping Sparrow (*Spizella passerina*)	CHSP	6.8 ± 4.45	10.2 ± 5.57	7	0.23	0.63
Swamp Sparrow (*Melospiza georgiana*)	SWSP	—	1.9 ± 1.91	1	1.00	0.32
White-throated Sparrow (*Zonotrichia albicollis*)	WTSP	19.4 ± 6.19	33.6 ± 6.35	25	2.55	0.12
Timber gleaners						
Red-breasted Nuthatch (*Sitta canadensis*)	RBNH	7.0 ± 4.50	V	4	2.42	0.13
Brown Creeper (*Certhia americana*)	BNCR	3.3 ± 2.52	1.9 ± 1.91	3	0.21	0.65
Black-and-white Warbler (*Mniotilta varia*)	BWWA	2.1 ± 1.49	13.3 ± 4.49	10	5.60	0.023
Tree-foliage searchers						
Blue-headed Vireo (*Vireo solitarius*)	BHVI	—	8.1 ± 4.85	3	2.79	0.10
Red-eyed Vireo (*Vireo olivaceus*)	REVI	2.1 ± 2.14	12.6 ± 4.23	8	4.87	0.033
Black-capped Chickadee (*Poecile atricapillus*)	BCCH	0.7 ± 0.71	V	1	1.00	0.32
Boreal Chickadee (*Poecile hudsonica*)	BOCH	0.7 ± 0.71	1.4 ± 1.43	2	0.20	0.66
Golden-crowned Kinglet (*Regulus satrapa*)	GCKI	16.2 ± 4.62	0.7 ± 7.14	13	11.03	0.002
Ruby-crowned Kinglet (*Regulus calendula*)	RCKI	3.1 ± 2.45	1.9 ± 1.91	3	0.15	0.70
Tennessee Warbler (*Vermivora peregrina*)	TEWA	3.3 ± 2.32	1.4 ± 1.43	3	0.49	0.49
Northern Parula (*Parula americana*)	NOPA	2.7 ± 1.50	0.2 ± 0.24	5	2.66	0.11
Magnolia Warbler (*Dendroica magnolia*)	MAWA	28.1 ± 5.78	31.0 ± 6.33	29	0.11	0.75
Cape May Warbler (*Dendroica tigrina*)	CMWA	V	2.4 ± 1.78	2	1.79	0.19
Yellow-rumped Warbler (*Dendroica coronata*)	YRWA	9.0 ± 3.41	1.0 ± 7.42	10	5.38	0.026
Blackburnian Warbler (*Dendroica fusca*)	BKWA	20.5 ± 6.57	3.3 ± 1.90	11	6.28	0.016
Canada Warbler (*Wilsonia canadensis*)	CAWA	—	10.5 ± 5.87	3	3.19	0.082

[a] Dashes indicate that the species was not recorded, either with a territory or as a visitor in the control.

TABLE 3. Selected habitat variables and associated correlations with each of three principal components having eigenvalues >1. PCA based on 2001 and 2002 data from 21 blowdown and 21 control cells, Superior National Forest, Minnesota.

Habitat variable	PC 1	PC 2	PC 3
% tree cover	0.43	−0.08	−0.08
No. dead trees/ha	0.17	−0.33	−0.54
Live tree diameter (cm)	0.40	−0.10	0.34
% shrub cover	0.35	−0.12	−0.06
No. live shrub stems/ha	0.32	0.53	0.00
No. dead shrub stems/ha	0.35	0.01	−0.18
% herb cover	0.17	−0.46	−0.06
% bryophyte cover	0.31	−0.14	−0.16
% coarse litter cover	0.18	−0.31	0.72
Coarse woody debris (m^3/ha)	−0.34	−0.51	−0.02

$F_{1,40}$ = 6.28, P = 0.016). Golden-crowned Kinglet (control: 16.2 ± 4.62, blowdown: 0.7 ± 7.14, $F_{1,40}$ = 11.03, P = 0.002) and Yellow-rumped Warbler (control: 9.0 ± 3.41, blowdown: 1.0 ± 7.42, $F_{1,40}$ = 5.38, P = 0.026; Table 2).

By foraging guild, 6 of the 14 (43%) species of ground-brush foragers and flycatchers held territories in the blowdown but not in the control; 6 of the 8 (75%) species holding territories in both blowdown and control had a greater percentage of territory cover in the blowdown than in the controls. Four of the 13 (31%) species of tree-foliage searchers had more territory cover in the control (all $P <$ 0.05). Only the Red-eyed Vireo had a greater percentage of territory cover in the blowdown (control: 2.1 ± 2.14, blowdown: 12.6 ± 4.23, $F_{1,40}$ = 4.87, P = 0.033; Table 2).

Three principal components had eigenvalues >1 (PC 1 = 3.71, PC 2 = 1.78, PC 3 = 1.18) and together explained 67% of the variance in the vegetation dataset. The first principal component explained 37% of the variance and was positively correlated with the diameter of live trees and tree cover, while being negatively correlated with the volume of debris (Table 3). The second component, which explained 18% of the variance, was positively correlated with the number of live shrub stems and negatively correlated with the volume of debris (Table 3). A plot of PC 1 versus PC 2 (not shown) revealed only slight overlap of blowdown and control cells, indicating that the 10 habitat variables retained for use with the CCA reasonably separate one type from the other.

The Monte Carlo permutations test conducted with the CCA indicated that both the first canonical function (P = 0.027) and the overall test (P = 0.010) were significant, with the correlation between selected species and habitat being relatively high (r = 0.84). The first axis of the CCA accounted for 9.9% of the variation in the bird data, and was positively correlated with the volume of debris (DEBRIS, r = 0.51) and negatively correlated with tree cover (CTREE, r = −0.72). Bird species preferring heavy cover at or near the ground with little to no canopy cover (Mourning Warbler, Chestnut-sided Warbler, Yellow-bellied Flycatcher, and Winter Wren) were positively correlated with the first axis—the volume of debris in particular—and are shown in the extreme right hand portion of Figure 2. Species such as the Golden-Crowned Kinglet, Blackburnian Warbler, Swainson's Thrush, and Northern Parula were negatively correlated with the first axis and preferred more tree cover (Fig. 2).

Although not significant, the second canonical function explained 5.0% of the variance in the bird data (Monte Carlo test: P = 0.21) and was positively correlated with bryophyte cover (CBRYO, r = 0.66) and herb cover (CHERB, r = 0.41). Birds most closely associated with bryophyte and herb cover included Nashville Warbler, Northern Parula, and White-throated Sparrow.

DISCUSSION

Our data suggest that the primary effect of the 4 July 1999 storm was a significant decrease in tree canopy and the diameter of live

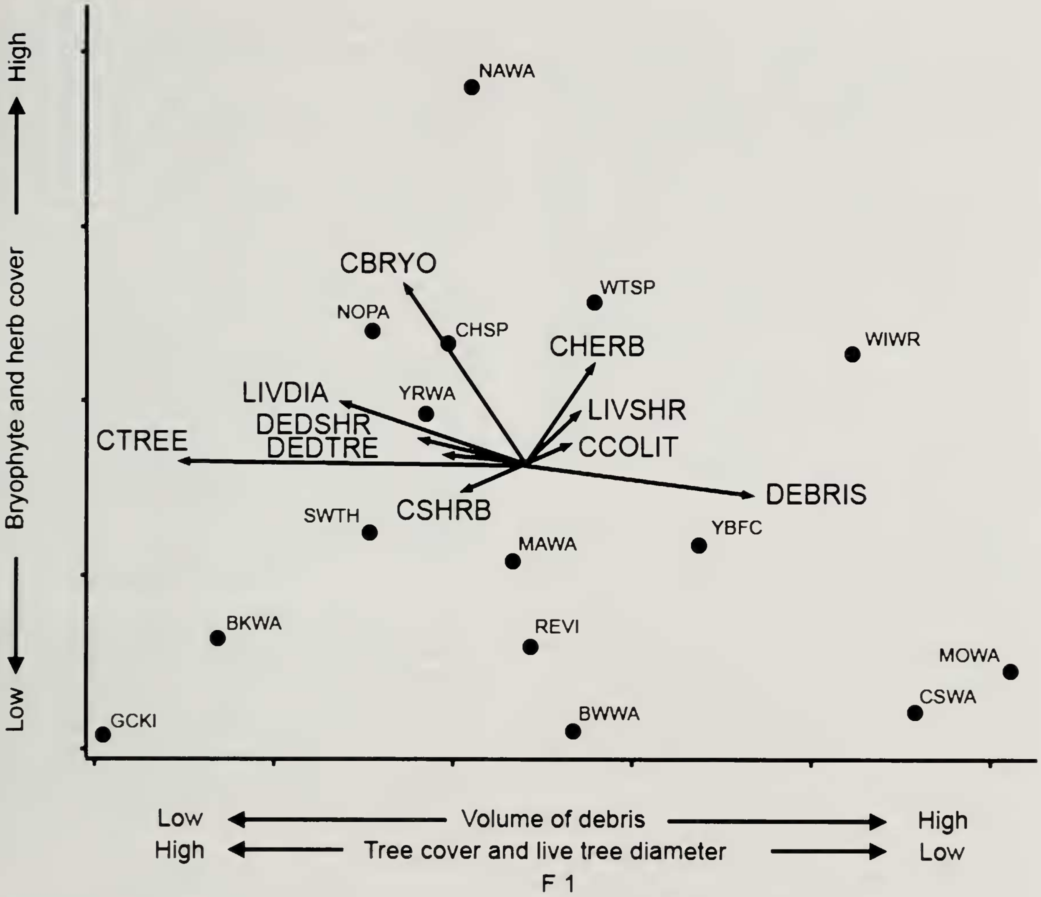

FIG. 2. Bird distribution and vegetation variables (2001, 2002 data) based on functions 1 (F1) and 2 (F2) of a canonical correspondence analysis of 10 vegetation variables (codes defined in Table 1) and 15 bird species (codes defined in Table 2) from 21 blowdown cells and 21 control cells following a catastrophic 1999 blowdown in a black spruce–balsam fir forest in the Superior National Forest, Minnesota. The length and direction of the vector for each habitat variable corresponds to the level of its correlation with each function.

trees, with a concomitant increase in shrub layer structure and coarse woody debris. Tree cover, which was generally characterized by black spruce, balsam fir, and paper birch (*Betula papyrifera*), was slightly greater in the pre-blowdown but reduced to half that of the control as a result of the windstorm. The wind also decreased the number of live trees and the diameter of both live and dead trees by blowing over or breaking off all but the largest dead trees and most of the bigger live trees. In the shrub layer, fallen trees and treetops eliminated disparities between disturbance and control plots with respect to shrub cover and the number of live shrub stems that existed before the storm by increasing the amount of cover at or near the ground in the blowdown area. Coarse woody debris in the blowdown area also increased significantly as a result of the storm.

Many researchers have documented the importance of coarse woody debris to avian communities (Davis et al. 1999, Greenberg and Lanham 2001, Lohr et al. 2002), citing increases in nest-site suitability and food availability as possible explanations (Lohr et al. 2002) for its importance. Chestnut-sided and Mourning warblers, which were strongly associated with the volume of coarse woody debris, are often associated with dense shrubbery and open woods of early successional forests (Apfelbaum and Haney 1981, Ehrlich et al. 1988, Schulte and Niemi 1998). Winter Wren was also associated with the low-canopy blowdown despite being typically associated with old-growth forests (Hejl et al. 2002). Yellow-bellied Flycatcher, White-throated Sparrow, and Black-and-white Warbler also showed some preference for areas with higher levels of coarse woody debris, with all but the White-throated Sparrow having significantly more territory cover in the blowdown. Red-eyed Vireo, a species often associated with closed-canopy or mature forest (James 1976, Faanes and Andrew 1983), also had significantly more territory cover in the blowdown but has been shown to respond better than expected to canopy loss (Greenberg and Lanham 2001, Faccio 2003).

Golden-crowned Kinglet and Blackburnian Warbler had significantly more territory cover in the control than in the blowdown and were highly correlated with the overall amount of tree canopy cover and the diameter of live trees (Fig. 2). Both species typically forage, and spend most of their time, high in the trees (Ehrlich et al. 1988, Morse 1994), and their numbers would likely decline if that stratum were reduced.

Overall, a significant decrease in tree canopy cover and the volume of coarse woody debris have provided more opportunities for species that forage or nest (or both) at or near the ground, while limiting opportunities for species more likely to use tree canopies. While these effects do parallel some of the responses to fire or timber-harvest disturbances, differences are apparent as well. Both wind and fire lead to a decline in tree canopy, greater numbers of snags, and an increase in ground and shrub-layer cover. After fire, however, trees often die slowly over several years, and, in the Great Lakes region, they may remain standing for several years before contributing to the volume of coarse woody debris. In contrast, severe wind resulted in an immediate decrease in tree cover and a corresponding increase in shrub-layer structure and coarse woody debris. Like the effects of wind, logging activities also result in a reduction of tree canopy and tree stem density, and an increase in coarse woody debris.

Similar to what we found after the windstorm, post-fire bird communities are typically distinguished by higher densities of flycatchers and ground-brush foragers and fewer tree-foliage searchers (Apfelbaum and Haney 1986, Drapeau et al. 2000, Morissette et al. 2002). The effect of logging on bird communities is largely dependent upon the number of residual trees and snags and the amount of coarse woody debris (Brawn et al. 2001, Lohr et al. 2002). Unlike fire or wind, relatively few snags remain after clear-cuts, which leads to a nearly complete change in avian community composition (Schieck and Hobson 2000, Brawn et al. 2001). Natural disturbances like wind, and arguably timber harvests in some cases, result in more heterogeneous landscapes as a result of different seral stages (Niemi et al. 1998), thereby enhancing the diversity of bird communities (Angelstam 1998, Brawn et al. 2001).

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